THE BREEDING BIOLOGY AND LARVAL DEVELOPMENT OF *HYLA JERVISIENSIS* (ANURA: HYLIDAE)

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(Plate I)

[Read 30th March, 1966]

Synopsis

The *Hyla ewingi* complex has had a confused taxonomic history. The present account provides a clear diagnosis of one member of the complex, *H. jervisiensis*, on the basis of morphology, mating call, breeding habits and a detailed study of larval development. The geographic distribution and relationships of *H. jervisiensis* are discussed and it is pointed out that the taxonomic situation is still not completely resolved.

Introduction

Hyla jervisiensis Dumeril and Bibron (*sensu* Moore, 1961) was, until recently, known only from a restricted area of coastal New South Wales (see Moore, 1961, p. 283, Fig. 56). In 1963, however, the presence of this species at two localities in eastern Victoria was discovered (Littlejohn, Martin and Rawlinson, 1963), and it has since been found at a third nearby location (15 miles N. of Orbost, Vic.). The previous southermost record was a questionable specimen from Lawler's Creek, near Bodalla, N.S.W. (Moore, 1961). Apart from this record the species had not been found south of Jervis Bay, N.S.W. Thus the Victorian specimens represent a range extension of at least 100, and possibly, 200 miles. The geographic distribution as known at present is indicated in Figure 1. Reference to earlier accounts of *H. jervisiensis* (Fletcher, 1889; Copland, 1957; Moore, 1961) revealed that virtually nothing was known of its biology. Since a considerable amount of information on the breeding biology has been gathered concomitantly with general distributional studies, the additional data are presented here.

Moore (1961) compared individuals of this species from the Sydney area (its known northern limit) with sympatric *H. verreauxi* Dumeril (as *H. ewingi* Dumeril and Bibron; see Littlejohn, 1963, 1965) with which it has often been confused. Our material was collected near the south-western limit of the known range of *H. jervisiensis*, where it is sympatric with *H. ewingi* (*sensu stricto*) as well as *H. verreauxi* (Littlejohn, 1965). Since *H. jervisiensis* shows a closer resemblance to *H. ewingi* than to *H. verreauxi*, comparison will be made with the former species.

While there is little doubt that the specimens considered in this paper are conspecific with *H. jervisiensis* of Moore (1961), we nevertheless have some reservations regarding the use of the name. Firstly, we have not been able to find *H. jervisiensis* (*sensu* Moore) at its supposed type locality (Jervis Bay, N.S.W.), nor, as far as we are aware, have any specimens apart from the type ever been collected there. Secondly, we have collected two specimens of another *Hyla* there, which we are unable to refer to any presently recognized form, but which show morphological evidence of relationship with the *H. ewingi* complex. We heard, but did not record, the mating call of one of these specimens, and again were unable to refer it to any described member of the *H. ewingi* complex, nor indeed to any other described *Hyla* inhabiting the area. Subsequent visits to the area have not resulted in the collection of further data

on this form. The situation requires detailed analysis; possibly it will necessitate the re-erection of *Hyla kreffti* Günther (whose type locality is Sydney, N.S.W.) to accommodate the taxon treated in this paper; the true *H. jervisiensis* perhaps being represented by our unidentified Jervis Bay specimens. It should be noted, however, that Moore (1961) examined the types of both *H. jervisiensis* and *H. kreffti*, and considered them to be identical. Hence, at this stage, no decision is warranted.

Materials and Methods

Mating calls were recorded in the field using an EMI L2B tape recorder and an AKG D19 dynamic microphone. The recordings were subsequently analysed on a Kay 6061-A sound spectrograph and/or a Cossor 1049 double beam oscilloscope. These two methods provided reasonably complete information on acoustic characteristics. Wet bulb air temperatures were taken at the calling sites.

Various developmental stages were collected in the field and, in some cases, further reared in the laboratory at room temperature (15·0–25·0°C), in enamel trays (approximately 33 × 21 × 4 cm.) containing pond water. Boiled lettuce was provided as food. In one instance fertilized eggs were collected and allowed to develop to an early larval stage, with a few being fixed every second day. On another occasion field collected larvae were taken through to metamorphosis to confirm their identity.

The descriptions, measurements and drawings are of preserved material. Adults were preserved in 70% alcohol, and larvae in 4% formalin or Tyler's (1962) fixative. Measurements were taken from mature adults and all available developmental stages, using vernier callipers reading to 0·05 mm. Drawings were made with the aid of a *camera lucida* attached to a stereoscopic microscope.

The staging system used in describing embryos and larvae is that of Gosner (1960).

Adult Morphology

As indicated in the introduction, the species most likely to be confused with *Hyla jervisiensis* is *H. ewingi* (*sensu stricto*). Moore (1961) included a table of differences between *H. verreauxi* (as *H. ewingi*) and *H. jervisiensis*, but

Table 1

Principal differences between Hyla jervisiensis *and* H. ewingi (sensu stricto) *from East Gippsland, Vic.*

		H. jervisiensis	*H. ewingi*
Body length	♀	58·2 mm.*	37·5 mm. (range 34·5–40·8)†
	♂	49·9 mm. (range 46·6–51·6)‡	35·0 mm. (range 33·2–37·0)‡
Tibia length/Body length ratio	♀	0·53*	0·48 (range 0·43–0·52)†
	♂	0·53 (range 0·50–0·54)‡	0·50 (range 0·47–0·52)‡
Light stripe below eye		Inconspicuous	Conspicuous
Texture of back		Usually warty	Smooth
Odour in life		Distinctive, curry-like	Not distinctive

* Based on 1 specimen.
† Based on 4 specimens.
‡ Based on 10 specimens.

most of the features listed will not distinguish *H. ewingi* proper from H. *jervisiensis*. Table 1 shows those of Moore's characters which are useful in diagnosis of *H. ewingi* as well as *H. verreauxi*, and also some other characters which we have found to be reliable. An adult male *H. jervisiensis* is shown in Plate 1, Figure 2 (see Littlejohn, 1963, for a figure of an adult *H. ewingi*).

The following key may be used to distinguish the three species in coastal south-eastern Australia :

1. Finger pads wider than fingers. Back patch not divided between the eyes. No spots on the groin 2
   Finger pads same width as fingers. Back patch divided between the eyes. Spots present on the groin. Body length of mature males less than 40 mm. ..... *H. verreauxi*
2. Conspicuous white stripe below the eye. No distinctive odour in life. Body length of mature males less than 40 mm. ..... *H. ewingi*
   No conspicuous white stripe below the eye. Odour in life curry-like. Body length of mature males more than 40 mm. ..... *H. jervisiensis*

Breeding Sites and Breeding Season

Four breeding sites were examined : Royal National Park, N.S.W. ; Bell Bird, Vic. ; 12 miles W. of Cann River, Vic. ; and 15 miles N. of Orbost, Vic. (Table 2). Only one of these sites (12 miles W. of Cann River) has been visited repeatedly, and the majority of the observations and collections were made

Table 2

Breeding sites of Hyla jervisiensis

Locality	Description	Date of Visit	Stages Present
Royal National Park, N.S.W.	Permanent stream in dense dry sclerophyll forest	May 24, 1960	Calling ♂♂
		August 20, 1962	Calling ♂♂
Bell Bird, Vic.	Permanent sluggish stream in open meadow	August 24, 1963	Calling ♂♂
12 miles W. of Cann River, Vic.	Series of small, temporary pools on road margin	August 24, 1963	Calling ♂♂, gravid ♀, eggs, larvae at stages 25–30
		November 3, 1964	Larvae in three size-classes, the largest being beyond stage 30
		January 14, 1965	Eggs
		March 6, 1965	———— (ponds dry)
15 miles N. of Orbost, Vic.	Large, permanent dam in dry sclerophyll forest	March 6, 1965	Newly metamorphosed juveniles

there. At Royal National Park, N.S.W., Moore (1961) heard males calling in February, and we heard them at this location in May and August. Fletcher (1889) collected gravid females at Burrawang, N.S.W., in July. It thus seems likely that *H. jervisiensis* is able to breed throughout the year, possibly being triggered by rainfall.

Mating Call Structure and Calling Behaviour

Recordings of three individuals and a chorus were obtained at the locality 12 miles W. of Cann River, Vic., on 24th August, 1963, together with those of one *H. ewingi*. Calls of only one *H. jervisiensis* were sufficiently clear of

those of other individuals to allow an accurate determination of all call characteristics ; the one *H. ewingi* could be similarly treated (Table 3). It was possible to determine only pulse repetition rate and dominant frequency in the calls of the other two *H. jervisiensis*, and the following values were obtained (at a wet bulb air temperature of 8°C) : Pulse repetition rate : 38·5 and 42·6 pulses/sec. ; Dominant frequency : 1650 and 1550 cycles/sec.

Audiospectrograms of part of a call of each species are presented in Plate 1, Figure 1.

The mating call of *H. jervisiensis* is basically like that of *H. ewingi* and consists of a series of similar, repeated notes, each of which is broken up into a number of clearly separated pulses, that is, fully modulated. The entire call of *H. jervisiensis* is longer, as is the note duration, and the note repetition rate is much lower. The pulse repetition rates are similar, but the dominant frequency of the call of *H. jervisiensis* is lower. The apparent similarity of pulse repetition rates is rather interesting, for calls of sympatric hylids are

Table 3

Physical characteristics of mating calls of a Hyla jervisiensis *and a* H. ewingi *recorded 12 miles W. of Cann River, Vic., on 24th August, 1963, at a wet bulb air temperature of 8·0°C.*

Data are based on three calls of one individual of each species and call note values are for the middle note of a call. Mean values are given with ranges in parentheses.

Call characteristic	*H. jervisiensis*	*H. ewingi*
Call duration (seconds)	9·1 (6·0–12·3)	3·9 (3·4–4·4)
Notes per call	10·7 (7–14)	15·0 (13–17)
Note repetition rate (notes per minute)	70·5 (68·3–73·3)	232·6 (229·2–237·0)
Note duration (seconds)	0·67 (0·64–0·70)	0·15 (0·14–0·15)
Pulses per note	25·7 (24–27)	6·0 (6)
Pulse repetition rate (pulses per second)	38·5 (37·5–39·4)	41·0 (40·0–42·9)
Dominant frequency (cycles per second)	1683 (1600–1750)	2390*

* Calculated from one call only.

usually well differentiated in this component (Littlejohn, 1965). Presumably the differing dominant frequencies minimize acoustic interference and allow for efficient auditory discrimination.

In Royal National Park, males were calling along a stream, from marginal vegetation 1–2 m. above the ground. At 12 miles W. of Cann River the frogs were calling from the shallow water at the edge of the ponds, from the ground near the ponds, and from a height of up to 1 m. in the vegetation 7–8 m. from the ponds.

Wet bulb air temperatures taken at the sites of calling males were 8·0 and 11·0°C.

Development

Oviposition and eggs.—The actual process of oviposition was not observed. The eggs, which are laid in small clusters attached to twigs or blades of grass, have dark brown animal hemispheres, creamy-white vegetal hemispheres, and individual jelly capsules. Within a cluster the eggs adhere to each other, and not all of them are attached directly to the supporting vegetation. Those that are attached appear to have short " stalks ", possibly due to the weight of the egg cluster stretching the jelly at the point of adhesion (Figure 2). The

number of eggs per cluster varies from 1–31, with a mean of 6·8 in the 18 clusters counted. The total egg complement of a single female is unknown.

A series of 10 early gastrulae (stage 10) had the following dimensions: embryo diameter, $2 \cdot 33 \pm 0 \cdot 02$ mm. (mean and standard deviation); capsule diameter, $7 \cdot 58 \pm 0 \cdot 64$ mm.

Pre-hatching embryos.—Cleavage and gastrulation appeared normal and were not closely studied. The first set of embryos examined in detail have a total length of about 4 mm., and are in stage 18 (Figure 3). They are dark grey to black, with the yolk sac slightly paler. The tail bud is bent sharply to the left, and separated from the yolk sac by a ventral notch. There is a slight stomodaeal depression between the arms of the U-shaped ventral sucker. The gill plate, auditory vesicle and pronephros are recognizable.

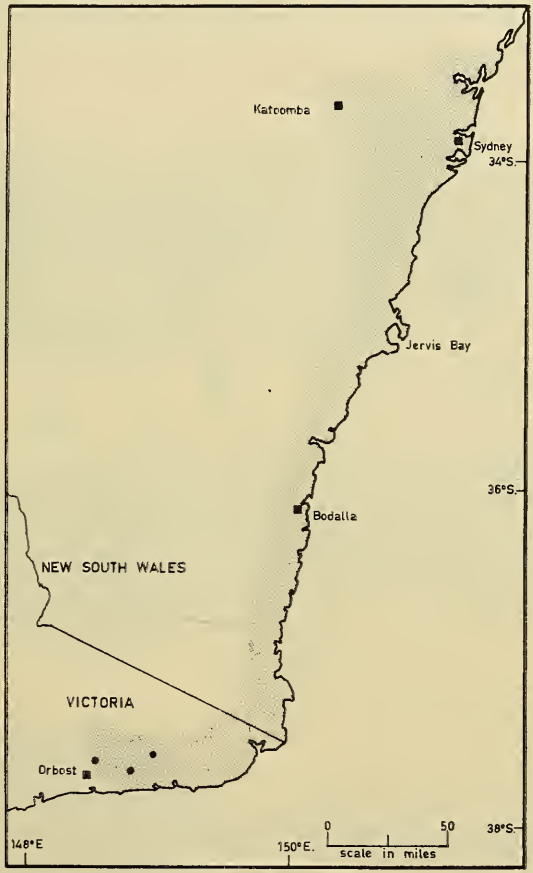

Fig. 1. The known geographic distribution (stippled) of *H. jervisiensis*. Only collecting localities additional to those of Moore (1961) are shown, and the positions of the type locality and some towns are indicated for reference.

Two days later the embryos are in stage 20, and have a total length of about 6 mm. (Figure 3). The overall colour is dark grey, but the tail fin is starting to become transparent. The stomodaeal depression is well-marked, and the ventral sucker has become separated into two portions, one at each side of the stomodaeum. Olfactory pits and optic bulges are visible. Two pairs of external gills are present, the anterior pair each having 4–5 branches, and the posterior pair 1–2.

Post-hatching embryos.—Hatching occurs at about stage 23 (Figure 3). Three individuals in this stage have total lengths of 8·8, 9·0 and 9·2 mm. There is little change in pigmentation, except that the tail fin is virtually transparent, and the cornea beginning to clear (the cornea is clear by stage 21 in Gosner's series, which is thus not precisely applicable to stages 21–23 of *H. jervisiensis*). The external gills are further developed, the anterior pair each having 4–5 branches, and the posterior pair 2–4. The mouth is open and the ventral suckers are still present. Embryos fixed 50 hours later are still in stage 23. The total length is about 10 mm. The operculum has almost completely covered the external gills on both sides, and the cornea is transparent. Ridges can be distinguished at the lateral and posterior margins of the mouth, foreshadowing the labial teeth and papillae.

Stage 24, in which the operculum closes on the right, was not observed. The next group of embryos fixed are in stage 25, when the operculum is fully closed and the spiracle visible. The horny jaws, labial papillae and labial

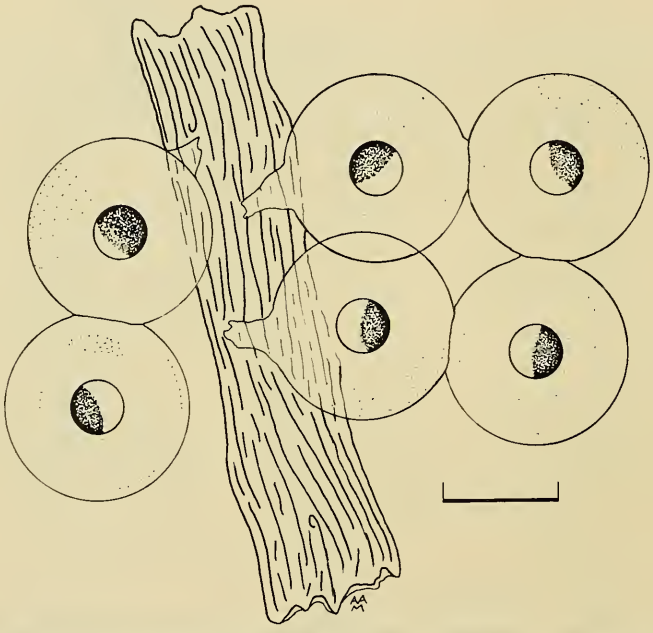

Fig. 2. Egg cluster of *H. jervisiensis*, 12 miles W. of Cann River, Vic. The bar represents 5 mm.

teeth, comprising the mouth disc, have also developed. During this stage the anus opens and the ventral suckers are lost. The mean dimensions of six embryos in this stage are : total length, 15·75 mm. ; body length, 6·24 mm. ; maximum body width, 3·80 mm.

Larvae.—The beginning of larval development is marked by the appearance of the hind limb buds in stage 26 (Limbaugh and Volpe, 1957). Apart from increase in size and progressive hind limb development, stages 26–40 are somewhat similar, and a description of a larva at stage 30 will suffice (Figure 3).

The overall body colour is dark brown, almost black. In ventral view the anterior half of the body is slightly lighter in colour. The myotomal area of the tail is darkly pigmented only along the dorsal edge, and is light brownish elsewhere. The tail fins are dusky, and blood vessels are clearly visible in the dorsal fin and posterior half of the ventral fin. The cornea is peculiar in having a somewhat greater diameter than the eyeball ; the eye thus appearing to be

surrounded by a light-coloured ring. The spiracle is sinistral and ventrolateral in position, and is not visible in a dorsal view of the larva. The anus is dextral. The external nares are raised on small papillae, and open in an anterior direction. Both dorsal and ventral tail fins are arched and moderately deep.

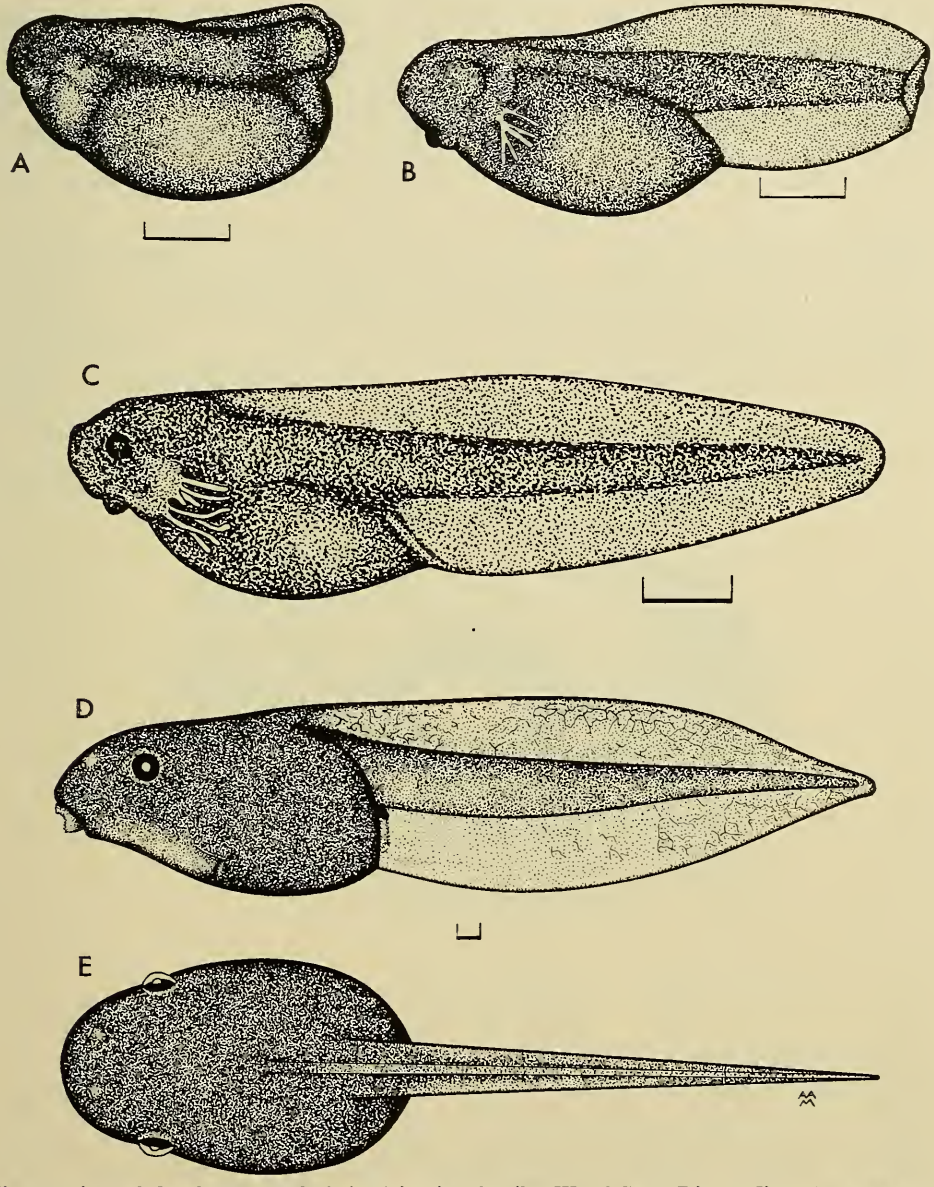

Fig. 3. Larval development of *H. jervisiensis*, 12 miles W. of Cann River, Vic. A : stage 18 ; B : stage 20 ; C : stage 23 (hatching) ; D and E : stage 30. The bar in each case represents 1 mm.

The mouth (Figure 4) is sub-terminal in position. The mouthparts appear to be fully developed by stage 27. Of the 14 larvae examined in stages 27–40, 12 have mouth discs virtually identical with that in Figure 4. The other two differ only in having a somewhat wider break in the second upper labial tooth row. The mouth is typically bordered by two to three rows of papillae, but at the corners of the mouth the papillae extend medially towards the jaws.

TABLE 4

Body dimensions (in mm.) and proportions of Hyla jervisiensis *larvae. (Means are given with ranges in parentheses.)*

Stage	No.	Total length	Body length	Tail length	Maximum Body width	Maximum mouth disc width	Body length / Total length	Body width / Body length	Mouth disc width / Body width
27	1	33·00	13·25	19·75	7·70	3·45	0·40	0·58	0·45
28	3	32·85 (29·60–37·30)	13·25 (12·00–15·30)	19·60 (17·60–22·00)	7·97 (7·05–9·35)	3·73 (3·65–3·85)	0·40 (0·39–0·41)	0·60 (0·59–0·61)	0·47 (0·41–0·52)
29	1	34·60	12·60	22·00	7·40	3·90	0·36	0·59	0·53
30	3	40·16 (38·00–44·00)	16·20 (15·10–17·80)	24·00 (22·80–26·20)	9·62 (8·20–10·85)	4·28 (4·20–4·40)	0·40 (0·40–0·41)	0·59 (0·54–0·62)	0·45 (0·41–0·51)
31	1	42·00	16·00	26·00	9·30	4·45	0·38	0·58	0·48
32	2	41·60 (40·00–43·20)	15·92 (15·20–16·65)	25·68 (24·80–26·55)	9·13 (8·45–9·80)	4·58 (4·50–4·65)	0·39 (0·38–0·39)	0·57 (0·56–0·58)	0·50 (0·47–0·53)
37	1	44·60	17·15	27·45	10·40	4·65	0·38	0·61	0·45
39	1	49·20	18·60	30·60	11·80	5·45	0·38	0·63	0·46
40	1	50·25	19·40	30·85	11·10	5·75	0·39	0·57	0·52

The mouth formula is $\frac{1 \quad 1}{1 \quad 1}$, all the tooth rows being of subequal length.
$\frac{\quad 2 \quad}{}$

The horny jaws are stout and have their inner margins serrated.

Body dimensions and proportions of larvae at stages 27–40 are presented in Table 4. Proportions remain relatively constant through this part of development, as noted by Limbaugh and Volpe (1957) for *Bufo valliceps*. The mean body proportions for all individuals in these stages are: body length/total length, $0{\cdot}391 \pm 0{\cdot}015$; body width/body length, $0{\cdot}591 \pm 0{\cdot}025$; mouth disc width/body width, $0{\cdot}475 \pm 0{\cdot}042$.

Metamorphosis.—Three juveniles which metamorphosed in the laboratory have body lengths of 15·6, 16·2, and 18·3 mm. Two field-collected juveniles (15 miles N. of Orbost, Vic.) have body lengths of 18·2 and 19·7 mm. The juveniles are dark brown dorsally; the characteristic back patch of the adult is recognizable in only two individuals. The throat is dusky brown and the belly off-white; the thighs have a white ventral surface and an orange posterior surface. The dorsal surface is finely warty, and the ventral surface is granular from the level of the pectoral girdle backwards.

In the laboratory metamorphosis occurred in December. Juveniles were collected in the field on 6th March.

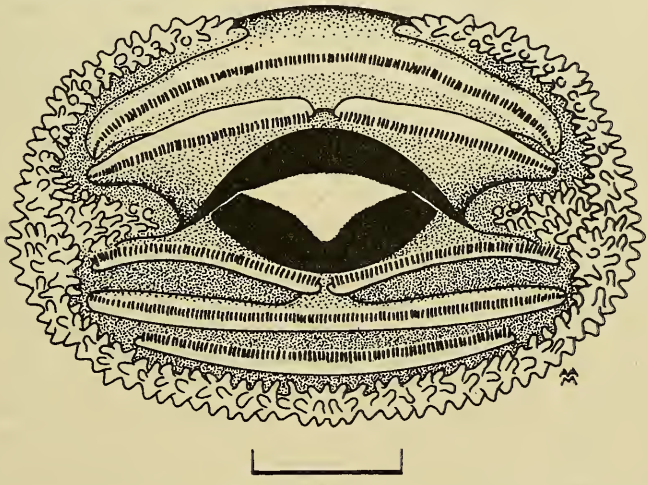

Fig. 4. Mouth disc of larva at stage 30 of *H. jervisiensis*. The bar represents 1 mm.

Larval life span.—No single individual has been reared from egg to metamorphosis, thus an exact figure for the duration of the larval life span is not available. A series of embryos took 14 days from egg to stage 25, while a group of larvae took 80 days from stage 30 to metamorphosis (at 15–25°C); thus the total span is probably in excess of 100 days. However, culture conditions in the laboratory may have been inadequate, so that under field conditions the development time could be shorter.

Discussion

Oviposition and eggs.—The habit of depositing eggs in small clusters seems to be fairly widespread among hylids. Examples of other species with this oviposition are: *H. caerulea*, 2000–3000 eggs in clusters of 100–200 each (Harrison, 1922); *Pseudacris streckeri*, 306–376 eggs in clusters of 2–14 each

(Fouquette and Littlejohn, 1960); and *Hyla regilla*, 500–1250 eggs in clusters of 5–60 each (Stebbins, 1962). However, there are also hylids which lay their eggs in a single mass, e.g. *H. phyllochroa* (Harrison, 1922) and *H. latopalmata* (Martin, ms.). The adaptive significance of these two types of oviposition pattern is not clear. Moore (1961, p. 173) suggests that scattering of eggs, i.e. depositing a few in each of several pools, is an adaptation to breeding in small, temporary bodies of water. Firstly, it provides for the contingency that some of the pools may dry out; and secondly, it prevents the possibility of the larvae being overcrowded. Another plausible hypothesis is that if the eggs are scattered in several masses there is less chance of a predator destroying the total egg complement. This point is discussed by Pyburn (1963).

The eggs of *H. jervisiensis* are unusually large (ovidiameter 2·33 mm.) among Australian hylids. For comparison, ovidiameters of some other Australian hylids are: *H. phyllochroa*, 1·2 mm.; *H. caerulea*, 1·44 mm. (Harrison, 1922); *H. ewingi*, 1·65 mm. (range 1·60–1·70); *H. aurea raniformis*, 1·30 mm. (range 1·25–1·35) (Martin, unpublished).

Larval morphology and adaptation.—H. jervisiensis tadpoles do not differ markedly in morphology from those of other Australian hylids which breed in still water. The ventrolateral, sinistral spiracle, dextral anus, fairly deep fins, and 2 | 3 mouth formula are all typical of Australian hylid larvae (Martin, ms. and unpublished). The pattern of life history is also typically hylid in character (Martin, ms.), and is shared by *H. ewingi*. However, the life histories of *H. jervisiensis* and *H. ewingi* differ considerably in detail, and provide further aid in diagnosing the species. *H. ewingi* lays smaller eggs (ovidiameter 1·65 mm.), without clearly defined separate capsules, in larger clusters (see Waite, 1929, p. 261, figure 188). *H. ewingi* hatchlings are smaller and have less well developed external gills (Martin, unpublished), and the larvae have relatively wider, lighter coloured bodies. The mouth discs of the two species also differ in proportions and in the arrangement of the labial papillae (Martin, 1965). Newly metamorphosed *H. ewingi* juveniles are smaller (body length 11·1–13·6 mm.; Martin, 1965).

The manner of oviposition suggests that the life cycle of *H. jervisiensis* may be adapted to ephemeral aquatic situations, such as the site 12 miles W. of Cann River, Vic. Water temperatures in the pools at this locality ranged from 9·5°C (about 2100 hours, 24th August, 1963) to 30·5°C (1430 hours, 14th January, 1965). Tolerance by the larvae of such thermal fluctuation is further evidence of adaptation to life in small, shallow bodies of water. However, anurans breeding in temporary water, even in mesic environments, are usually characterized by rapid larval development. Examples are *Pyxicephalus adspersus* and *Lechriodus fletcheri*, each having a larval life span of about 31 days (Balinsky, 1957; Moore, 1961). There is no suggestion that the larval life span is abbreviated to this extent in *H. jervisiensis*, a species which is not limited to temporary water situations for breeding (Table 1). Further studies are necessary to establish the normal duration of the larval phase of this species in the field.

Acknowledgements

The authors acknowledge the support of the University of Melbourne Research Grant to the Zoology Department. Most of the field and running costs were met by a grant from the Nuffield Foundation to the second author (M.J.L.). The cooperation of the Australian Museum, Sydney, in allowing us to examine their collections from this area, is gratefully acknowledged.

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EXPLANATION OF PLATE I

Fig. 1. Audiospectrograms of part of a call of A, *H. jervisiensis* ; and B, *H. ewingi* ; recorded 12 miles W. of Cann River, Vic.

Fig. 2. Adult male *H. jervisiensis* from 12 miles W. of Cann River, Vic.